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A STUDY OF CAPTURES OF TRICHOPTERA IN A LIGHT TRAP NEAR READING, BERKSHIRE

By M. I. Crichton

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With 10 Text-figures

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I. Introduction

For many years light traps have been used for the capture of nocturnal insects. Most frequently they are used simply to obtain specimens, especially Lepidoptera, for collections, and to study geographical distribution. It was Williams (1939, 1940), in an analysis of collections made nightly over four years, who demonstrated the value of the light trap in the study of insect ecology. From his collections he derived much information on seasonal distribution and the effect of weather conditions on the activity of insects. He devised the Rothamsted trap, using an ordinary electric lamp covered by an opaque roof which prevents rain entering the collecting jar (Williams, 1948). More recently, the Robinson trap, with a mercury vapour lamp, has been widely used by entomologists. As this trap has no protecting roof, the light is directly visible both from above and laterally (Robinson and Robinson, 1950). In tests designed to compare these traps Williams (1951), and Williams, French and Hosni (1955), have shown that the mercury vapour lamp attracts more insects, of all orders, than the ordinary electric lamp, and that the Robinson trap catches more of the heavier, strongly flying insects, while the Rothamsted trap catches more of the small insects.

Over the four years, 1933–36, Williams captured about 850,000 insects in his trap at Rothamsted. Of these, 87 per cent. were Diptera, 10 per cent. were Lepidoptera, while, in the remaining 3 per cent. which represented all the other orders, there were only 256 Trichoptera and 10 Ephemeroptera. The scarcity of these aquatic insects was accounted for by the absence of ponds and streams in the vicinity. When, however, a light trap is set up beside a lake or river, it attracts very large numbers of

Trichoptera, Ephemeroptera and aquatic Diptera, and smaller numbers of other aquatic insects.

It is of interest to note that McLachlan (1884) made what must be one of the first references to electric light as an attraction to Trichoptera. In Paris, on the occasion of the Fête Nationale, he recorded " a multitude of insects " attracted to the light of four carbon arc lamps in the Place de la Concorde. These insects were almost entirely Trichoptera, mostly Leptoceridae. Very few workers have operated a light trap, close to water, with the object of making regular collections of caddis flies. Kuwayama (1934) used a light trap to determine the flight period of two species of leptocerids in Japan. Marshall (1939) published a study of the Trichoptera of western Lake Erie, based on about 70,000 specimens of 47 different species collected at light near the lake. Milne (1943) made some use of a light trap in a study of the distribution and life history of caddis flies from a lake in Saskatchewan. Recently, Corbet and Tjønneland (1955) have published a detailed study of the nocturnal flight activity of 12 species of caddis flies at Lake Victoria, Uganda, based on light trap captures split into successive 10 minute periods throughout the hours of darkness.

As the information on the seasonal occurrence of British Trichoptera given in various local lists and in Mosely (1939) is scattered and incomplete, it is not always easy to know when to search for a given species. For the English Lake District, Kimmins (1943) published useful notes on seasonal occurrence which were based on regular sweeping and searching. Among areas which have been covered by local lists are Oxford (Grensted, 1935), Yorkshire (Brown and Whitehead, 1938), Derbyshire (Brown, 1938) and Northumberland (Philipson, 1957). A detailed study of the biology of a single species, *Athripsodes aterrima* (Stephens), by Morgan (1956), gives the flight period based on catches in floating emergence traps.

Recently Brindle (1956, 1957*a*, *b*) has used light at a number of sites in Lancashire and Yorkshire at different times of the year and has published records of Trichoptera and observations on their behaviour, and attraction to light. So far as I am aware, however, a light trap has not been used in this country for the regular collection of caddis flies throughout their flight period. The present work, which is based on regular counts over several years at one site, provides more information than has hitherto been available on the seasonal occurrence of a number of species.

II. Acknowledgments

This work was made possible through the kindness of Michael Milne-Watson, Esq., C.B.E., of Oakfield, in the parish of Wokefield, Berkshire, who allowed me to operate the trap at Millbarn Pond. Not only did he, and his family, endure the constant visits and interruption of their privacy, but he changed the trap and made weather observations during my absences for two weeks in August 1954 and 1955. I am also indebted to Mr. M. J. Oldland for help during these periods.

I wish to thank Dr. C. B. Williams for useful advice and discussion, and also Mr. D. E. Kimmins, who has always been most helpful in confirming identifications. I am greatly indebted to Professor Alastair Graham for his constant encouragement and interest. I am also grateful to my colleague, Mr. G. Williams, for help with the statistical analysis. Finally, I thank my wife for much help with the manuscript.

III. Site

Millbarn Pond was formed in the eighteenth century by building a dam across the alluvial valley of Lockram Brook. This small brook has its source about two miles away on the plateau gravel area of Burghfield, southwest of Reading. The pond has an area of eight and a half acres, and lies about 200 feet above sea level. The bottom is of deep black mud with deposits of decaying leaves near the bordering trees. The average depth of 4–5 feet, which increases to about 8 feet near the dam, is normally

kept fairly constant by the use of sluice boards at the outflow. The water is hard and the pond can be classed as eutrophic. The pond is fringed with trees and is roughly rectangular, with the dam across the north-eastern end, where there is a thick hedge of yew, and a plantation of big trees, mostly oak (fig. 1). Because of the shelter of these trees, high air and water temperatures are recorded in sunny weather. The only aquatic vegetation is a thick bank of bulrush along the NW side and some patches of water lilies. Lockram Brook leaves the pond at one end of the dam through a sluice and over brick-built steps into the tree-shaded valley below. Only in very wet weather is there any considerable outflow of water.

The light trap was placed on the ground near one end of the dam, very close to the surface of the water, and visible over the whole area of the pond. Its position is marked at A in figure 1. In 1957 a second trap was operated concurrently at position B, about 70 yards away, where, because of trees and the fall of the ground, the light was not visible from any part of the pond.

IV. Apparatus, Technique and Dates of Trapping

The light trap was the Robinson type, with a mercury vapour lamp of 80 watts connected to the main AC electricity supply by about 150 yards of cable. The necessary choke and Venner time switch were installed at the supply end. The time switch was set to turn the lamp on at sunset and off at sunrise. Each morning the trap was taken to the laboratory where the catch was counted.

The caddis flies were found to be alive and the majority were resting under the egg trays which had been placed inside the trap. The catch was anaesthetised with ether so that some of the flies could be used alive for the study of their mouth parts, while others were marked and released at the pond. The counting was usually done straight away, but when this was not possible the catch was preserved and dealt with later.

As far as possible, all caddis flies were identified, sexed and counted. On some nights, however, such large numbers of tiny hydroptilids were captured that direct counting was impracticable. While in 1953 no attempt was made to count them, in 1954 and 1955 the whole mass of tiny insects was collected up, by a suction pump., and weighed. A sample of convenient size was then weighed and all the caddis flies in it were identified and counted. An estimate of the total catch was thus calculated. Mayflies were preserved for later examination, and record was also kept of many of the other insects captured.

In the autumn of 1957, when two traps were in operation, in addition to the Trichoptera all the insects were counted and assigned to their orders. A further difference in procedure was the use of a bag of terylene net curtaining inside the trap in place of the egg trays. The bag was closed with a draw string when taken out of the trap and placed in a large killing bottle, so that there was no need to transport the whole light trap each time to the laboratory.

In 1953, the trap was in use about every third night from 26th May until 13th December, but no trapping took place between 27th July and 20th August. Furthermore, as already explained, the small hydroptilids were not counted, so that the 1953 records are not fully comparable with the regular collections made in 1954 and 1955. Caddis flies were already active by the starting date, 26th May, and the last night on which they were captured was 14th/15th November. In 1954, the trap was in operation every third night from 18th April until 24th November, except for three occasions when the electricity was accidentally cut off. Caddis flies were captured first on the night of 30th April/1st May and for the last time on 11th/12th November. In 1955, the trap was in use every third night from 21st April until 6th December. It was on the night of 27th/28th April that caddis flies were caught for the first time, and on 23rd/24th November for the last time. In 1957, two traps were in operation every night from 12th September until 23rd November.

V. Meteorological Records

Air and water temperatures were recorded at position A (fig. 1) each night the trap was in use during 1954, 1955 and 1957. Two minimum thermometers, divided to 0·5° C., were carried on a framework of " Dexion " angle strip arranged so that one recorded air temperatures 10 inches above water level, and the other water temperature 20 inches below water level. The thermometers were read when the trap was set up and again when it was collected. It was thus possible to obtain an approximate record of the temperature range during the time of trapping, as well as the minimum night temperature. In the autumn of 1957 a recording thermo-hygrograph was set up on open ground at position C. A continuous record of temperature and relative humidity was thus secured for every night in this trapping period.

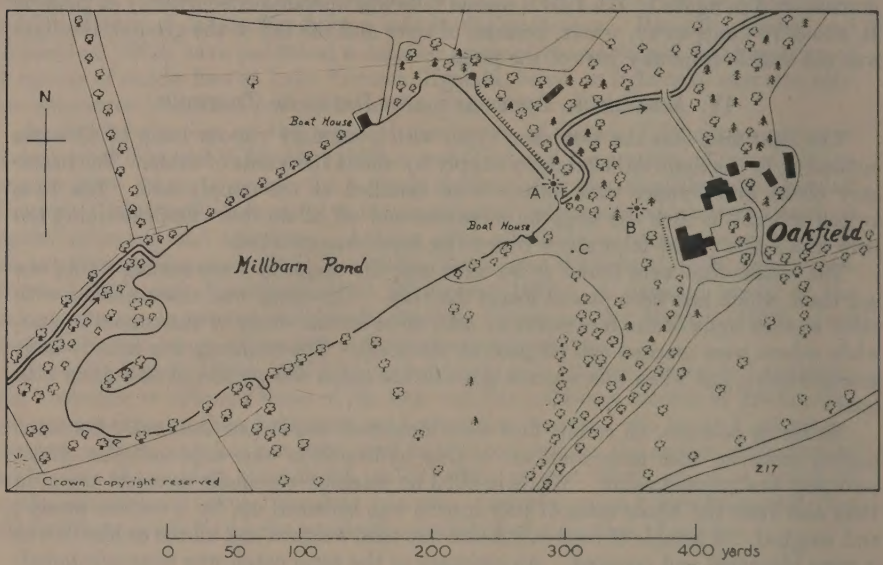

Fig. 1.—Map of Millbarn Pond and its immediate surroundings. A, waterside site of light trap on dam in 1953, 1954, 1955 and 1957. B, field site of second light trap in 1957. C, position of recording thermohygrograph and raingauge in 1957.

(Reproduced from the Ordnance Survey map, scale 1 : 2500.)

I am indebted to Mr. Philip L. D'E. Skipwith for records of daily rainfall in 1953, 1954 and 1955, taken at Grazeley Green, 164 feet above sea level, within one mile of Millbarn Pond (Station No. 791 in the British Rainfall Organization). For the autumn of 1957 a raingauge was set up beside the thermohygrograph at position C. Daily record was kept of the general state of the weather.

VI. Species Captured

The species of Trichoptera, and the numbers captured in the four years, are listed in Table I. The arrangement and nomenclature are based on Mosely (1939), with the Limnephilidae revised as proposed by Kimmins (1956). To this total of 69 species may be added a single specimen of the hydroptilid, *Allotrichia pallicornis* (Eaton) caught on the night of 25th/26th August, 1952, before regular trapping was started. The one specimen of *Plectrocnemia* sp. and four specimens of *Agapetus* sp., which were all females, were not identified beyond the genus. Many of the identifications have been confirmed by Mr. D. E. Kimmins, and examples of all the species have been preserved.

In the course of recent collecting, 94 species of Trichoptera have been recorded for the county of Berkshire (Crichton, Baker and Hanna, 1956, 1957; Crichton and Baker, 1959), and to this can be added 11 species found by earlier collectors. Thus the light trap at Millbarn Pond has yielded 70 of the 105 species so far recorded for the county. This catch of 70 represents just over one-third of the species of caddis flies recorded for the whole of Great Britain. In this connection it may be noted that Williams (1939), in four years trapping at Rothamsted, collected just over one-third of the species of Macrolepidoptera known in Britain.

It would be interesting to know if similar ponds in other parts of the country would yield as many species if subjected to the same intensive collecting. Although some of the caddis flies may have come from other bodies of water, there is no doubt that the main source of all these flies was Millbarn Pond itself. The larvae of most of the species recorded are found normally in lakes and ponds. There were no representatives of the families Beraeidae, Odontoceridae and Philopotamidae, whose larvae are found usually in fast-flowing streams.

Because of the depth and muddy bottom of the pond, collecting of larvae was difficult. A lot of time could have been spent in the search for larvae of species which came to the light trap in only small numbers. Larvae of the following species were found and identified: *Phryganea grandis*, *P. striata*, *Limnephilus flavicornis*, *L. lunatus*, *Anabolia nervosa*, *Halesus radiatus*, *Molanna angustata*, *Athripsodes aterrima*, *Mystacides longicornis*, *Triaenodes bicolor*, *Leptocerus tineiformis*, *Cyrnus* sp., *Agraylea* sp., *Orthotrichia* sp. and *Oxyethira* sp.

VII. Numbers

The totals of about 66,000 caddis flies in 1954 and 43,000 in 1955 are comparable because the trap was in use every third night over the same period from April to November. The 1953 total excludes the hydroptilids, and is based on a shorter period of irregular trapping. Only a few hydroptilids were caught in 1957 because trapping took place in the autumn after their main active season. During this autumn period, however, there were two traps in use every night. Thus, although the total catches in 1953 and 1957 are not directly comparable with the others, the collected results over the four years do give an indication of the relative abundance of the different species of caddis flies.

By far the most abundant species was *Oxyethira costalis*, of which over 80,000 were captured in the two years 1954 and 1955. Over the same period the catch of the next commonest species, *Orthotrichia tetensii*, was about 13,000. In 1953, this species and species of *Hydroptila* were not recorded as notes were kept only of the abundant *Oxyethira costalis* and of the two species of *Agraylea*. The next most abundant species was *Mystacides longicornis*, of which over 4,000 specimens were caught. Large counts were also recorded of *Limnephilus lunatus*, *Leptocerus tineiformis* and *Hydropsyche angustipennis*, while many species were represented by catches of several hundreds. There were 13 species of which only a single specimen was captured over the whole period of trapping. The single male of *Ironoquia dubia* is only the fourth specimen of this species to be recorded in Britain (Crichton and Baker, 1959). Thus, there was an appreciable number of rare species and the bulk of the catch was composed of only a few species. This common feature of any wild population, or sample of one, is discussed by Williams (1954), who developed from it the concept of an index of diversity. I am indebted to him for examining the data from Millbarn Pond for 1953, 1954 and 1955 and deriving from it the index of diversity as shown in Table II.

TABLE I.—*Numbers of the species of Trichoptera captured at Millbarn Pond in the years* 1953, 1954, 1955 *and* 1957

Species	1953	1954	1955	1957	Total
PHRYGANEIDAE					
Phryganea grandis L.	10	27	77	.	114
P. striata L.	24	26	29	.	79
P. varia F.	.	5	3	.	8
LIMNEPHILIDAE					
Ironoquia dubia (Steph.)	.	.	.	1	1
Limnephilus flavicornis (F.)	393	293	130	118	934
L. marmoratus Curt.	7	5	3	26	41
L. politus McL.	1	.	.	.	1
L. decipiens (Kol.)	.	.	.	1	1
L. lunatus Curt.	952	1,310	259	809	3,330
L. griseus (L.)	3	.	.	2	5
L. bipunctatus Curt.	1	.	.	1	2
L. affinis Curt.	.	.	.	3	3
L. hirsutus (Pict.)	.	1	.	.	1
L. centralis Curt.	1	.	.	.	1
L. sparsus Curt.	26	15	17	49	107
L. auricula Curt.	39	44	27	226	336
L. vittatus (F.)	96	33	8	71	208
L. extricatus McL.	.	1	2	1	4
Grammotaulius atomarius (F.)	4	2	2	5	13
Glyphotaelius pellucidus (Retz.)	186	79	61	54	380
Anabolia nervosa (Curt.)	20	45	9	34	108
Halesus radiatus (Curt.)	8	12	2	31	53
H. digitatus (Schr.)	96	263	26	162	547
Stenophylax permistus McL.	56	10	8	126	200
S. lateralis (Steph.)	2	.	2	.	4
S. sequax (McL.)	4	5	4	8	21
Chaetopteryx villosa (F.)	.	.	.	1	1
SERICOSTOMATIDAE					
Goëra pilosa (F.)	.	.	11	.	11
Silo pallipes (F.)	2	.	2	.	4
S. nigricornis (Pict.)	1	.	.	.	1
Brachycentrus subnubilus Curt.	.	1	.	.	1
Lepidostoma hirtum (F.)	.	2	.	.	2
MOLANNIDAE					
Molanna angustata Curt.	5	19	17	.	41
LEPTOCERIDAE					
Athripsodes fulva (Ramb.)	6	.	2	.	8
A. senilis (Burm.)	46	82	128	.	256
A. aterrima (Steph.)	32	14	89	.	135
A. cinerea (Curt.)	69	149	602	.	820
A. albifrons (L.)	.	.	18	.	18
A. dissimilis (Steph.)	64	16	247	.	327
Mystacides azurea (L.)	1	1	11	.	13
M. longicornis (L.)	175	1,961	2,005	18	4,159
Triaenodes bicolor (Curt.)	2	10	20	.	32
Adicella reducta (McL.)	.	1	.	.	1
Oecetis ochracea (Curt.)	19	29	197	2	247
O. furva (Ramb.)	.	1	.	.	1
O. lacustris (Pict.)	25	307	360	1	693
Leptocerus tineiformis Curt.	53	415	2,239	.	2,707

TABLE I.—*continued*

Species	1953	1954	1955	1957	Total
HYDROPSYCHIDAE					
Hydropsyche angustipennis (Curt.)	50	317	1,108	1	1,476
H. contubernalis McL.	23	4	40	.	67
H. instabilis (Curt.)	13	2	91	9	115
Cheumatopsyche lepida (Pict.)	.	1	.	.	1
POLYCENTROPIDAE					
Neureclipsis bimaculata (L.)	.	.	1	.	1
Plectrocnemia sp.	.	1	.	.	1
Polycentropus flavomaculatus (Pict.)	26	3	38	.	67
Holocentropus picicornis (Steph.)	.	1	5	1	7
Cyrnus trimaculatus (Curt.)	7	21	36	.	64
C. flavidus McL.	.	.	81	.	81
PSYCHOMYIDAE					
Ecnomus tenellus (Ramb.)	22	223	230	12	487
Tinodes waeneri (L.)	50	155	82	88	375
Lype phaeopa (Steph.)	.	18	5	.	23
Psychomyia pusilla (F.)	10	.	79	.	89
RHYACOPHILIDAE					
Rhyacophila dorsalis (Curt.)	5	3	4	1	13
Agapetus sp.	.	1	2	1	4
HYDROPTILIDAE					
Agraylea multipunctata Curt.	++	*c.* 650	232	.	*c.* 882
A. pallidula McL.	+	33	465	1	499
Hydroptila sparsa Curt.	.	.	83	.	83
H. pulchricornis (Eaton)	.	15	123	.	138
Orthotrichia tetensii Kolbe	++	*c.* 4,573	*c.* 8,829	.	*c.* 13,402
Oxyethira costalis (Curt.)	+++	*c.* 55,340	*c.* 25,311	78	*c.* 80,729
	c. 2,635	*c.* 66,545	*c.* 43,462	1,942	*c.* 114,584

Note.—In 1953 the hydroptilids were not counted and some species were undoubtedly overlooked; + signifies that a species was present, ++ that it was present in moderate numbers, and +++ that there were very large numbers.

TABLE II.—*The index of diversity of light trap catches at Millbarn Pond (Hydroptilidae are excluded)*

Year	Number of individuals	Number of species	Index of diversity
1953	2,635	43	7·1
1954	5,934	46	6·9
1955	8,419	47	6·8
Totals	16,988	59	7·6

The diversity in each of the three years is remarkably uniform, and, as expected, is greatest in the total catch.

In Table III the numbers of the species of caddis flies are grouped in a geometric series. Williams (1954), who grouped the numbers of individuals per species in this way for 240 species of Macrolepidoptera from his light trap at Rothamsted, showed a peak in the 5–13 and 14–40 classes. The Millbarn Pond figures in Table III give evidence of one peak in the 14–40 or 41–121 class and another in the first class of one individual per species. Thus these catches of caddis flies appear to have yielded an

unusual number of single specimens of species, especially in 1954. Some of these species are probably rare because the pond is an unsuitable habitat for the larvae, while others may well have flown from other breeding sites.

TABLE III.—*Numbers of individuals of species of caddis flies in* 1953, 1954 *and* 1955 *grouped in* ×3 *geometric classes* (*Hydroptilidae are excluded*)

Number of individuals per species	Number of species in each class			
	1953	1954	1955	Total
1	5	10	1	11
2–4	6	6	11	6
5–13	9	6	7	8
14–40	10	10	10	5
41–121	9	4	7	13
122–364	2	7	7	7
365–1093	2	1	1	5
1094–3280	.	2	3	3
3281–9841	.	.	.	1*
Total species	43	46	47	59

* The figures in this column represent the sum of individuals in the three years, so that there was one species [*Mystacides longicornis*] with a total within the 3281–9841 group (4141 individuals, see Table I) but not enough in any one year to be included in one of the individual year columns.

VIII. Sex Proportions

The species of which more than 100 specimens were caught are listed in ascending proportion of females in Table IV. Of the 26 species listed, 16 exhibit an excess of males, five an approximate equality of the sexes (40 per cent. to 60 per cent. females) and five an excess of females. Williams (1939) has demonstrated a wide variation in the sex ratio for many Lepidoptera and Diptera, but for most species more males than females were attracted to his light trap. It must, of course, be remembered that the proportion of sexes caught in a light trap is not necessarily the same as in the field population from which they have been drawn. The light trap catches are an indication of the relative activity of the two sexes and of their reaction to light. A departure from the expected equality of the sexes at the time of emergence cannot be deduced from light trap captures alone.

Some species of leptocerids form dense swarms close to the water and along the shores of lakes and streams. These swarms, which are composed mainly of males, are formed on quiet warm days and are often conspicuous on still evenings. Morgan (1956), in his study of the biology of *Athripsodes aterrima* in Perthshire, collected the emerging adults in floating traps ; in 1954, he caught 166 males and 97 females, the females thus representing 37 per cent. of the total. He considered that an initial preponderance of males may be connected with the swarming habit of this species. *A. aterrima* was represented in the light trap at Millbarn Pond by 106 males and 29 females, a female proportion of 21 per cent. *Mystacides longicornis* was often seen in large swarms at Millbarn Pond, and out of a total catch of over 4,000, only 20 per cent. were females. On the other hand, *Athripsodes cinerea*, which was also seen in swarming flight, showed approximate equality of the sexes (52 per cent. females). At the other extreme, in the same family, was the small species *Leptocerus tineiformis*, not observed in swarming flight, with 80 per cent. females. In contrast, the family Limnephilidae exhibited a marked uniformity in sex proportions ; of 6,302 captured, only 22 per cent. were females. Excluding the 11 species of which less than ten specimens were caught, the remaining 13 species were represented by between five per cent. and 31 per cent. females.

A trap so close to the water might be expected to catch approximately equal numbers of males and females of small weakly flying species—if there is equality of the sexes at emergence. The catches of *Tinodes waeneri* (58 per cent. females), *Ecnomus tenellus* (60 per cent. females), and *Oxyethira costalis* (61 per cent. females)

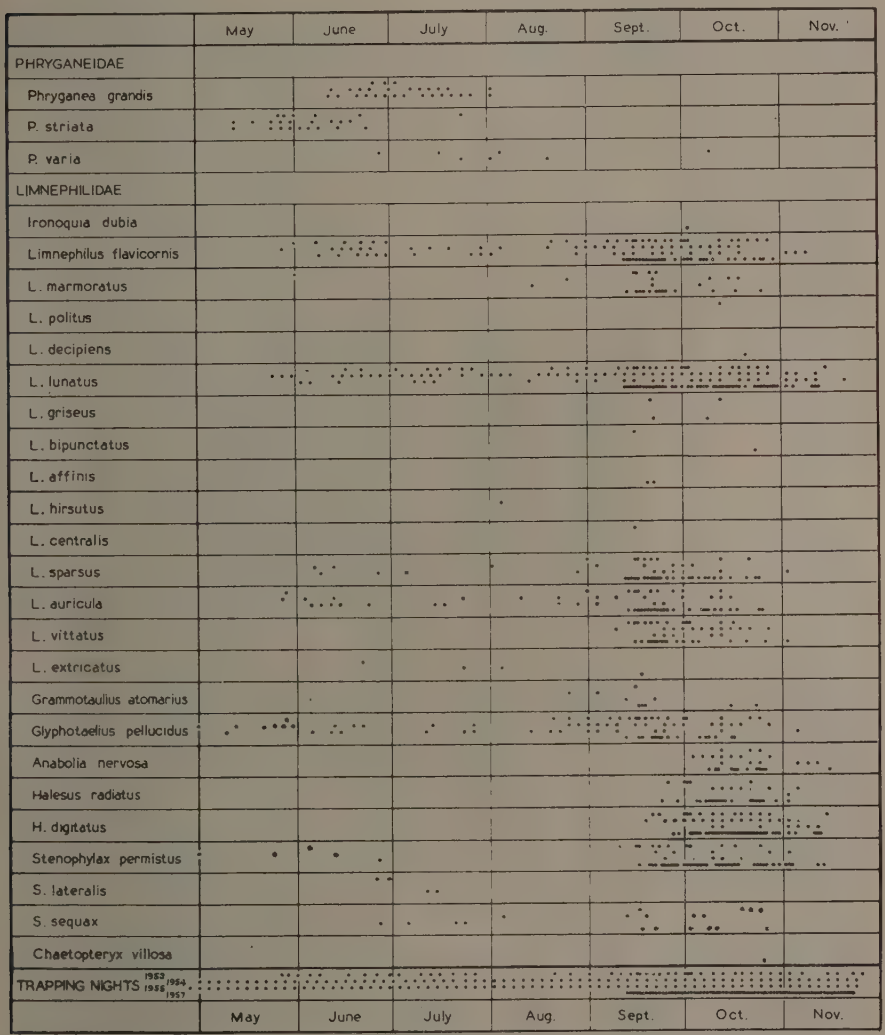

FIG. 2.—Dates of capture of Phryganeidae and Limnephilidae in the years 1953, 1954, 1955 and 1957. The key at the foot of the figure shows the nights when the light trap was in operation.

could be explained in this way. It should be noted, however, that the proportion of sexes varied greatly on different nights. Reference to the sex proportions of *O. costalis* in figure 6 shows that there was a preponderance of males during the early part of the swarming period of the first generation. In 1954, up to 25th May, the female proportion was 14·6 per cent. and in 1955 to the same date it was 15·1 per cent. In the catches after this date, the proportion of females rarely fell below 70 per cent.

On the other hand, a constant feature of all catches of *Orthotrichia tetensii* was the high proportion of females, 94·7 per cent. in 1954, and 95·3 per cent. in 1955. This is a small species of hydroptilid which is unlikely to fly far from water. If there is not an excess of females at the time of emergence there must be a striking difference

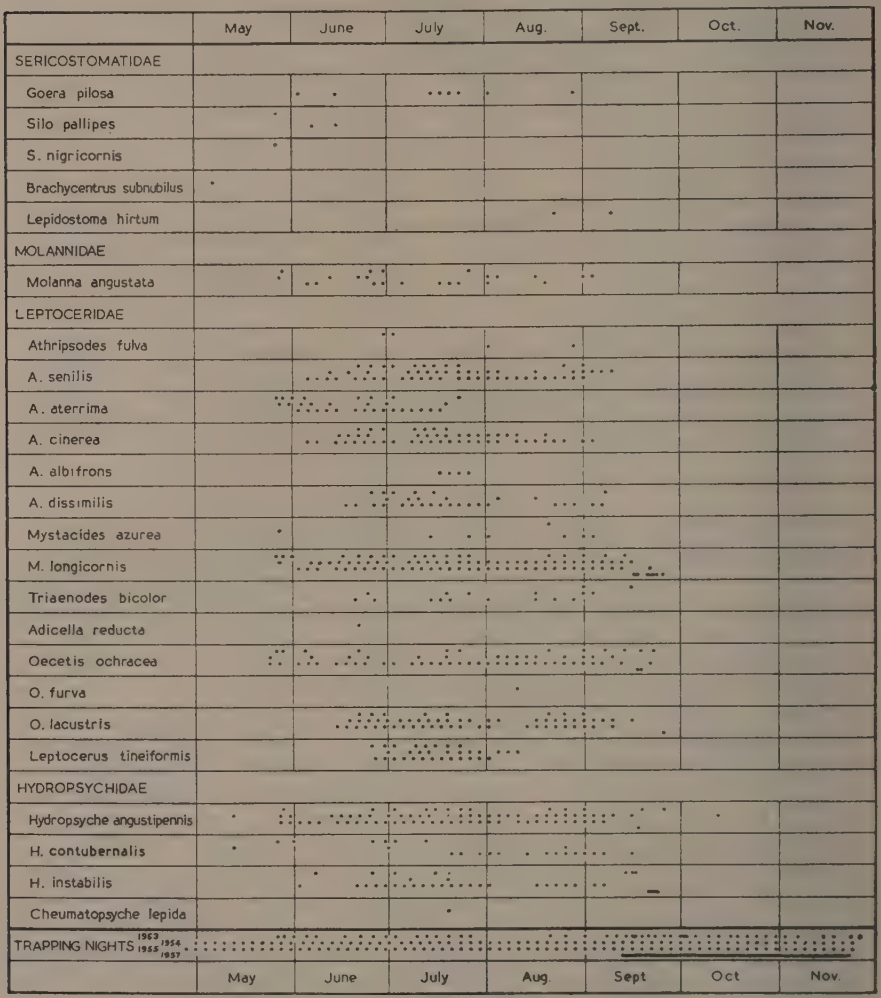

FIG. 3.—Dates of capture of Sericostomatidae, Molannidae, Leptoceridae and Hydropsychidae in the years 1953, 1954, 1955 and 1957. The key at the foot of the figure shows the nights when the light trap was in operation.

between the sexes in either behaviour or reaction to light. Females were also predominant in the catches of *Hydropsyche angustipennis* (65 per cent.), *H. contubernalis* (88 per cent.), and *H. instabilis* (91 per cent.).

Marshall (1939) recorded wide variation in the sex ratio of six species of caddis flies caught at light on the shores of Lake Erie. In one species, *Psychomyella flavida*, of 1,785 captures all were females.

TABLE IV.—*Sex proportions of Trichoptera, of which more than* 100 *specimens were captured in the four years, arranged in order of ascending percentage of females. All specimens captured were sexed, except those species marked *, where only a sample of the catch was sexed.*

Species	♂♂	♀♀	Percentage ♀♀
Limnephilus sparsus	99	8	7
L. auricula	307	29	9
Anabolia nervosa	94	14	13
Glyphotaelius pellucidus	330	50	13
Phryganea grandis	98	16	14
Halesus digitatus	465	82	15
Mystacides longicornis	3,317	842	20
Athripsodes aterrima	106	29	21
**Agraylea pallidula*	383	105	22
**A. multipunctata*	463	130	22
Limnephilus vittatus	161	47	23
L. flavicornis	720	214	23
Athripsodes senilis	189	67	26
Limnephilus lunatus	2,454	876	26
Stenophylax permistus	137	63	31
Oecetis ochracea	155	92	37
O. lacustris	336	357	52
Athripsodes cinerea	394	426	52
A. dissimilis	137	190	58
Tinodes waeneri	156	219	58
Ecnomus tenellus	197	290	60
**Oxyethira costalis*	6,359	9,811	61
Hydropsyche angustipennis	519	957	65
Leptocerus tineiformis	533	2,174	80
Hydropsyche instabilis	10	105	91
**Orthotrichia tetensii*	99	1,908	95

IX. SEASONAL OCCURRENCE

The results of four years trapping are displayed in figures 2, 3 and 4, where the capture of a species on a given night is recorded as a dot. The numbers of some of the commoner species are given in Tables V and VI, where the catches are grouped in 10-day periods. With this information it is possible to build up a fairly reliable picture of the seasonal occurrence of these species. This has been done under the following headings: (1) summer species; (2) autumn species; (3) double-brooded species. To complete the picture of the life history of a species regular collections of larvae and pupae are also needed. This is especially important when captures of adults suggest that a species has more than one brood in the year.

(1) *Summer Species*

Species which were captured in maximum numbers from May to August are regarded as summer species. Those with a short period of flight activity will be considered first.

Both *Phryganea grandis* and *P. striata* exhibited a short flight period. From Table V it can be seen that each year *P. striata* was most abundant at the end of May, while *P. grandis* reached its peak at the beginning of July. It is interesting that there should be this difference between two closely related species living in the same habitat.

The family Leptoceridae is represented by 14 species. The fact that these are summer species is shown clearly in figure 5, where the total catch of Leptoceridae is compared with that of Limnephilidae. The small caddis fly, *Leptocerus tineiformis* (Table VI), was almost entirely restricted to July, with a pronounced peak in the

middle of the month. This peak of activity took place over the same few days each year. The large catch on the night of 15th/16th July 1953 was not counted, but is represented by + in the appropriate space in Table VI.

Athripsodes aterrima was restricted to two months, from late May. In Perthshire, Morgan (1956) showed that emergence of this species began in the second week of June, with a peak in early July, and ended in early August. These observations were made in 1954 at the small sheltered Loch Dunmore, 350 feet above sea level.

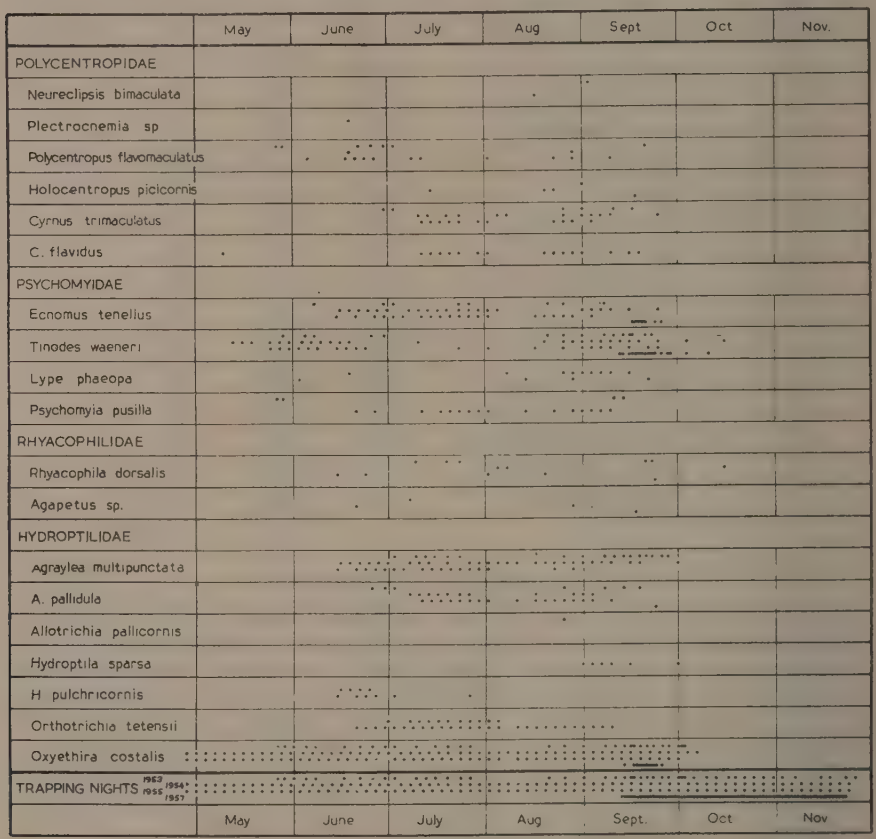

FIG. 4.—Dates of capture of Polycentropidae, Psychomyidae, Rhyacophilidae and Hydroptilidae in the years 1953, 1954, 1955 and 1957. The single specimen of *Allotrichia pallicornis* caught in 1952 is also included. The key at the foot of the figure shows the nights when the light trap was in operation.

At the larger and exposed Loch Moraig, at an altitude of 1,105 feet, he found that emergence was about a month later. In both lochs the mean daily water temperature was about 16° C. at the start of emergence, continuing at this level in the smaller loch but falling somewhat in the larger one towards the end of the period. Flight activity of this species at Millbarn Pond, as shown in the light trap records, began and finished about two weeks earlier than at Loch Dunmore. The water temperature over this period in 1954 at Millbarn Pond also averaged about 16° C. *A. cinerea* was caught over a rather longer period, as were the related species *A. senilis* and *A. dissimilis*.

TABLE V.—*Catches of selected species of Phryganeidae and Limnephilidae, grouped in 10-day periods.* (Note: xxx *indicates that no trapping took place*; — *indicates that no specimens were caught.*)

		26.iv–6.v	6.v–16.v	16.v–26.v	26.v–5.vi	5.vi–15.vi	15.vi–25.vi	25.vi–5.vii	5.vii–15.vii	15.vii–25.vii	25.vii–4.viii	4.viii–14.viii	14.viii–24.viii	24.viii–3.ix	3.ix–13.ix	13.ix–23.ix	23.ix–3.x	3.x–13.x	13.x–23.x	23.x–2.xi	2.xi–12.xi	12.xi–22.xi
Phryganea grandis	1953	xxx	xxx	xxx	—	—	—	10	—	—	—	xxx	—	—	—	—	—	—	—	—	—	—
	1954	—	—	—	—	1	4	5	12	4	1	—	—	—	—	—	—	—	—	—	—	—
	1955	—	—	—	—	12	4	18	34	6	3	—	—	—	—	—	—	—	—	—	—	—
P. striata	1953	xxx	xxx	xxx	20	1	2	—	—	1	—	xxx	—	—	—	—	—	—	—	—	—	—
	1954	—	1	5	15	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	1955	—	1	1	21	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Limnephilus flavicornis	1953	xxx	xxx	xxx	2	2	5	4	—	—	—	xxx	6	7	11	257	63	27	3	6	—	—
	1954	—	—	—	5	48	13	—	2	2	3	4	3	15	36	10	85	56	11	—	—	—
	1955	—	—	—	—	2	4	2	1	—	3	—	—	3	7	60	26	14	4	—	4	—
	1957	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	2	63	35	9	3	6	—	—
L. lunatus	1953	xxx	xxx	xxx	1	—	6	2	1	5	2	xxx	3	20	1	442	79	270	50	57	—	13
	1954	—	—	1	6	26	10	5	7	4	10	7	17	13	104	37	237	435	291	81	19	—
	1955	—	—	—	1	4	—	—	4	—	—	1	—	3	2	67	47	49	21	10	48	2
	1957	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	2	167	266	113	119	125	15	2
Glyphotaelius pellucidus	1953	xxx	xxx	xxx	1	—	—	—	—	—	—	xxx	12	17	4	120	19	7	2	4	—	—
	1954	2	2	2	8	1	2	—	1	—	2	—	—	4	16	3	24	8	3	1	—	—
	1955	—	1	—	—	3	—	—	3	2	1	1	2	2	7	28	7	2	—	—	2	—
	1957	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	1	18	21	12	2	—	—	—
Anabolia nervosa	1953	xxx	xxx	xxx	—	—	—	—	—	—	—	xxx	—	—	—	—	—	12	5	3	—	—
	1954	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	23	1	—	—
	1955	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	1	5	—
	1957	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	—	—	—	18	6	9	—	1
Halesus digitatus	1953	xxx	xxx	xxx	—	—	—	—	—	—	—	xxx	—	—	—	3	12	30	38	12	—	1
	1954	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	18	126	60	19	38	—
	1955	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	—	2	14	—
	1957	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	—	—	3	35	67	46	10	1

TABLE VI.—*Catches of selected species of Leptoceridae, Hydropsychidae, Psychomyidae and Hydroptilidae, grouped in 10-day periods.* (Note: xxx *indicates that no trapping took place;* — *indicates that no specimens were caught.*)

		26.iv–6.v	6.v–16.v	16.v–26.v	26.v–5.vi	5.vi–15.vi	15.vi–25.vi	25.vi–5.vii	5 vii–15.vii	15.vii–25.vii	25.vii–4.viii	4.viii–14.viii	14.viii–24.viii	24.viii–3.ix	3.ix–13.ix	13.ix–23.ix	23.ix–3.x	3.x–13.x	13.x–23.x
Athripsodes aterrima	1953	xxx	xxx	xxx	24	—	2	5	—	1	—	xxx							
	1954	—	—	—	8	3	1	1	—	1	—	—	—	—	—	—	—	—	—
	1955	—	—	—	25	13	16	10	18	7	—	—	—	—	—	—	—	—	—
A. cinerea	1953	xxx	xxx	xxx	—	—	—	56	4	3	—	xxx	—	—	1	—	—	—	—
	1954	—	—	—	—	—	22	—	13	31	63	19	1	—	—	—	—	—	—
	1955	—	—	—	—	36	80	108	117	134	96	5	21	4	1	—	—	—	—
Mystacides longicornis	1953	xxx	xxx	xxx	20	—	31	16	9	30	7	xxx	3	51	7	1	—	—	—
	1954	—	—	—	3	26	195	24	88	229	185	119	109	493	466	24	—	—	—
	1955	—	—	—	102	82	213	81	147	213	242	83	394	373	74	1	—	—	—
Leptocerus tineiformis	1953	xxx	xxx	xxx	—	—	—	12	18	23+	—	xxx	—	—	—	—	—	—	—
	1954	—	—	—	—	—	—	3	51	278	30	53	—	—	—	—	—	—	—
	1955	—	—	—	—	—	—	30	1307	824	78	—	—	—	—	—	—	—	—
Hydropsyche angustipennis	1953	xxx	xxx	xxx	4	—	—	3	2	10	1	xxx	12	16	—	1	1	—	—
	1954	—	1	—	10	5	28	2	22	10	21	66	20	52	73	6	—	1	—
	1955	—	—	—	120	204	121	97	127	147	208	22	45	12	5	—	—	—	—
Ecnomus tenellus	1953	xxx	xxx	xxx	—	2	—	8	—	1	3	xxx	4	1	3	—	—	—	—
	1954	—	—	—	—	—	34	27	33	72	7	36	—	2	10	1	1	—	—
	1955	—	—	—	—	1	6	29	64	74	12	—	29	12	3	—	—	—	—
Tinodes waeneri	1953	xxx	xxx	xxx	2	1	—	2	—	—	—	xxx	5	19	6	15	—	—	—
	1954	—	2	5	13	5	3	—	1	—	—	—	1	20	88	13	1	2	1
	1955	—	—	1	22	28	5	—	—	1	1	—	1	5	14	3	1	—	—
Agraylea multipunctata	1954	—	—	—	—	—	72	17	17	3	25	*c.*302	21	89	86	17	1	—	—
	1955	—	—	—	—	1	87	64	13	13	42	—	11	1	—	—	—	—	—
A. pallidula	1954	—	—	—	—	—	—	—	22	5	1	—	1	3	1	—	—	—	—
	1955	—	—	—	—	—	—	—	80	172	19	1	121	69	3	—	—	—	—
Orthotrichia tetensii	1954	—	—	—	—	—	—	27	*c.*715	*c.*2670	*c.*57	*c.*1104	—	—	—	—	—	—	—
	1955	—	—	—	—	—	17	75	*c.*2677	*c.*4487	*c.*1201	25	132	171	44	—	—	—	—

Mystacides longicornis was a common species at Millbarn Pond, forming swarms over the water on quiet evenings. The flight period extended from the end of May until the middle of September, with large catches towards the end of this period. The less abundant leptocerid, *Oecetis ochracea*, exhibited a similar extended flight period. *Hydropsyche angustipennis* is an example from another family of a summer species with a very long flight period.

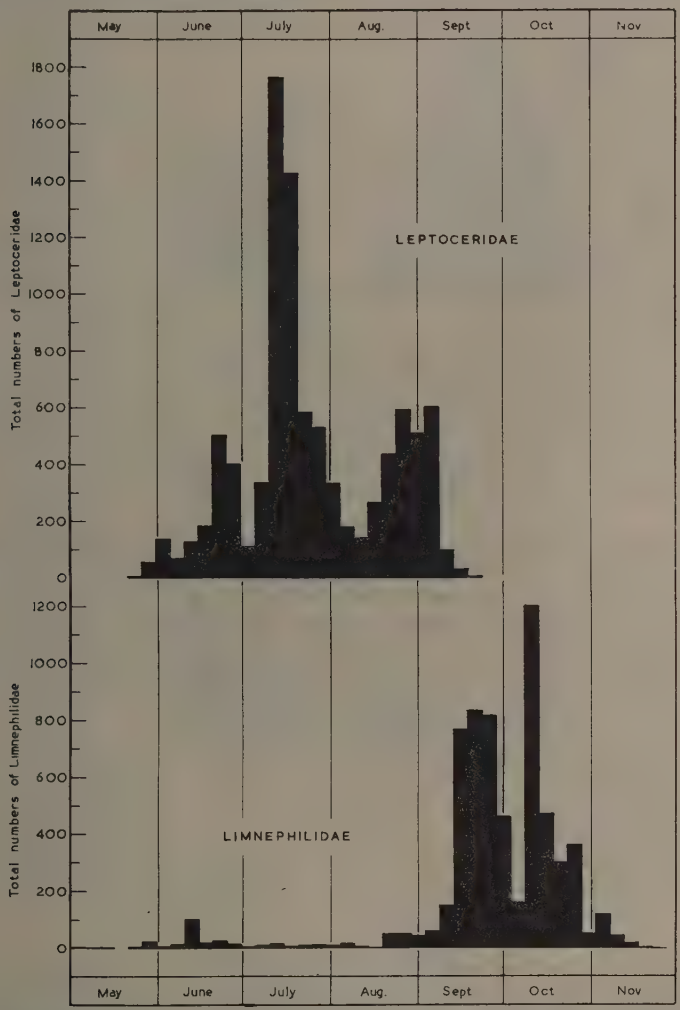

FIG. 5.—Total numbers of all species of Leptoceridae and Limnephilidae captured in the years 1953, 1954, 1955 and 1957, grouped in 5-day periods.

(2) *Autumn Species*

In contrast to other families, the Limnephilidae were caught mainly in the months of September and October (figure 2). This autumnal emergence is well shown in figure 5 in contrast to the summer emergence of the Leptoceridae. Further study of figure 2 reveals that the following species were caught only in September, October and November: *Ironoquia dubia, Limnephilus politus, L. decipiens, L. griseus, L. bipunctatus, L. affinis, L. centralis, L. vittatus, Anabolia nervosa, Halesus radiatus,*

H. digitatus and *Chaetopteryx villosa*. Excluding those species represented by only a few specimens, there were 208 *L. vittatus*, 108 *A. nervosa*, 53 *H. radiatus* and 547 *H. digitatus* caught in these three months. Of these four species, *L. vittatus* and *A. nervosa* have been recorded also in the summer months elsewhere in the Reading area (Crichton, Baker and Hanna, 1956, 1957; Crichton and Baker, 1959), and by other collectors in different parts of the country. On the other hand, *H. radiatus* and *H. digitatus* appear to be confined to these autumn months and this is confirmed in the local lists quoted in the introduction. The numbers of *Anabolia nervosa* and *H. digitatus* are shown in Table V.

Autumn would thus appear to be the normal emergence time for many Limnephilidae. Mosley (1939) records a number of species as autumnal, and the same pattern is seen in many local lists. From the results of general collecting, Botosaneanu (1957) arranges the Trichoptera of Roumania into three groups according to their period of flight. The autumn group is composed almost entirely of Limnephilidae, but he also records a number of species of this family as restricted to the summer.

Hanna (1959) studied the life cycles of *Limnephilus flavicornis*, *L. lunatus* and *Potamophylax stellatus* (Curt.) in the Reading area by taking regular monthly samples of larvae and pupae over two years. He showed for all three species an initial growth of the young larvae in October and November, with practically no increase in size until growth was resumed in March and April. In the Basingstoke Canal, where his collections were made, Hanna found only young larvae of *L. flavicornis* and *L. lunatus* during the winter, and pupae in increasing numbers from early June until early October. As the pupal stage lasts for three to four weeks, adults were emerging from July onwards, with largest numbers in September and October. There was clearly only one generation each year and no overwintering full-grown larvae were found at this site.

The catches of *Limnephilus flavicornis*, *L. lunatus* and *Glyphotaelius pellucidus* at Millbarn Pond, shown in Table V, demonstrate the small numbers of adults in May and June, compared with the main autumnal emergence. A similar pattern of catches was recorded for *Limnephilus sparsus*, *L. auricula* and *Stenophylax permistus*. Some of these summer specimens can be expected to have come from larvae which had overwintered in full-grown condition. Proof of such overwintering is given by Hanna for *Potamophylax stellatus*, in the River Pang, where he collected small numbers of full-grown larvae and pupae throughout the winter months.

From regular collections of larvae and pupae in the Manchester area, Hanna (1957) has recorded observations on the life cycles of *Limnephilus marmoratus*, *L. politus* and *Anabolia nervosa*. He showed that *A. nervosa* followed a similar course of development to that described above for *L. flavicornis* and *L. lunatus*. On the other hand, he collected pupae and adults of *L. marmoratus* and *L. politus* in June and July, and found that the larvae had grown appreciably before the winter months.

(3) *Double-brooded Species*

There is no evidence that any of the larger caddis flies discussed so far pass through more than one generation in the year. Among the smaller species collected in adequate numbers there are three, *Tinodes waeneri*, *Oxyethira costalis* and *Agraylea multipunctata*, which appear to be double-brooded. From figure 4 and Table VI it can be seen that *Tinodes waeneri* was caught in May and June and again from late August until October. In the years 1953, 1954 and 1955 only three out of a total of 287 specimens were captured in July and early August. These records suggest that *T. waeneri* is double-brooded, but for confirmation regular collections of larvae would be necessary. On the other hand, from the data available *Ecnomus tenellus* appears to be single-brooded, but it is possible that other species of Psychomyidae, all of small size, may be double-brooded.

Hanna (1959) collected larvae and pupae of *Agapetus fuscipes* Curt. in all months of the year, and adults in every month except January and February. This small caddis fly undoubtedly has more than one generation in the year, but Hanna was unable to separate the different generations with the information at his disposal. The light trap catches are of no assistance here as only four females belonging to this genus were collected.

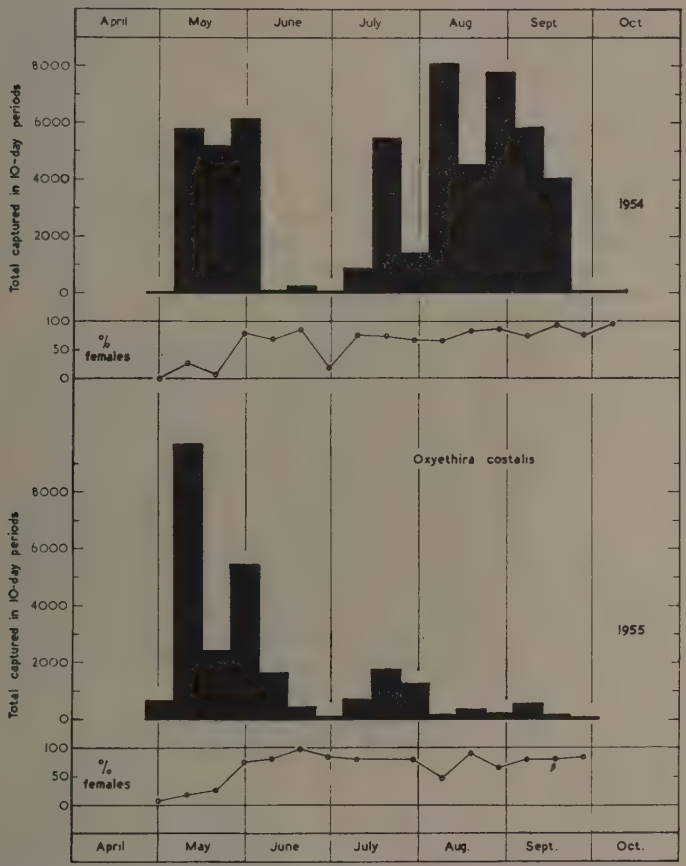

FIG. 6.—Captures of *Oxyethira costalis* in the years 1954 and 1955. Totals for 10-day periods are shown, with the sex proportions during these same periods.

Marshall (1939), on the basis of light trap collections during a single season, suggested that five species from Lake Erie were double-brooded. The two peaks recorded for these species were not always clearly separated, and smaller catches in the intervening period may have been due to unfavourable weather conditions. Milne (1943), working in Saskatchewan, recorded only one brood for three of these species. His conclusions were based on collections of larvae and pupae, and on the use of both sweep net and light trap for catching adults.

The family Hydroptilidae includes the smallest species of caddis flies, several of which are thought to complete more than one generation in the year. The tiny *Oxyethira costalis* was caught at Millbarn Pond in far greater numbers than any other caddis fly (see Table I), and for a period of just over five months. In 1953, its presence was recorded from the start of trapping on 27th May until 3rd October.

In 1954 it was one of the first species of caddis fly to be caught. From 1st May it was recorded every trapping night until 7th October. In 1955 it was the first species to be caught, on 28th April, and it was present in the trap every night except two until 1st October. Of many very large catches, the largest was on 5th August 1954, when it was estimated that there were nearly 7,000 individuals of this species. The numbers of *Oxyethira costalis*, grouped in 10-day periods, are shown in figure 6. In both 1954 and 1955, after large catches in May, there was a period of about one month from the beginning of June when catches were very small. Numbers increased again in July to give a second peak in August and September in 1954, but this build-up was not recorded in 1955. In his study of the development and biology of Hydroptilidae in Denmark, Nielsen (1948) found that the larvae of *Oxyethira costalis* passed through the winter in the nearly full-grown state and thus gave rise to adults in May and June. He was unable to find final instar larvae or pupae in the early part of July, but collected adults again in August. From his observations Nielsen concluded that there were two distinct generations of *O. costalis* rather than either a prolonged swarming period of one generation or the co-existence of two stocks with different swarming times. It would thus appear that there are two generations of *O. costalis* at Millbarn Pond. The earlier swarming periods could be explained by the milder winter conditions in Berkshire as compared with Denmark.

In 1954, an estimated total of 650 *Agraylea multipunctata* was captured between 16th June and 1st October, while in 1955 the catch was 232 between 15th June and 29th August (Table VI). The distribution of these catches suggests that this is a single-brooded species with maximum numbers from late June until the end of August. However, on 24th April, 1955, when setting up the trap at 15.10 hours in warm sunshine, I found a single specimen of this species. More specimens were found, close to the water, on 27th and 30th April and on 3rd May. Thus, while adults of *A. multipunctata* were present in the field as early as the end of April they were not captured in the light trap until 15th June. This night, with a minimum temperature of 14·7° C., was the first warm trapping night in 1955; on all previous nights except one the minimum temperature had been less than 10° C. In 1954, the first few catches of this species were made on nights which were noticeably warmer than those preceding. In contrast, *O. costalis* appears to have a greater tolerance for low temperatures as it was captured in large numbers on colder nights in May.

The above results demonstrate the limitations of light trap data used on their own in the study of life histories. Failure to capture a given species in spring and early summer, when night temperatures are often low, cannot be taken as proof of its absence. Nielsen (1948) concluded that *Agraylea multipunctata* passed through two generations in the year; it resembled *O. costalis* except that the larvae were all full-grown by the end of October. When the light trap captures of *A. multipunctata* are considered together with the evidence above of its presence in April and May at Millbarn Pond, it appears possible that the species may be double-brooded here as in Denmark.

Another hydroptilid which Nielsen considered to be double-brooded in Denmark was *Hydroptila femoralis* (Eaton), whereas two other species, *Orthotrichia tetensii* and *Ithytrichia lamellaris* Eaton, he described as single-brooded. The records of *O. tetensii* from Millbarn Pond (see fig. 4 and Table VI), 1st July to 5th August in 1954 and 21st June to 10th September in 1955, likewise suggest a single brood, with maximum numbers in July. The other three species of hydroptilids, *Agraylea pallidula*, *Hydroptila sparsa* and *H. pulchricornis*, which were caught in smaller numbers, appeared likewise to be single-brooded.

X. Effect of Weather Conditions

The number of insects captured in a light trap is determined both by the size of the population present and by the activity of the insects. In the preceding section,

the commoner species of caddis flies from Millbarn Pond were grouped according to the time of year when they were captured. This period extended from the end of April until the beginning of November. As already recorded in the introduction, the trap was operated both before and after this period, and occasional search was also made for caddis flies during the winter months. It appears unlikely that any of

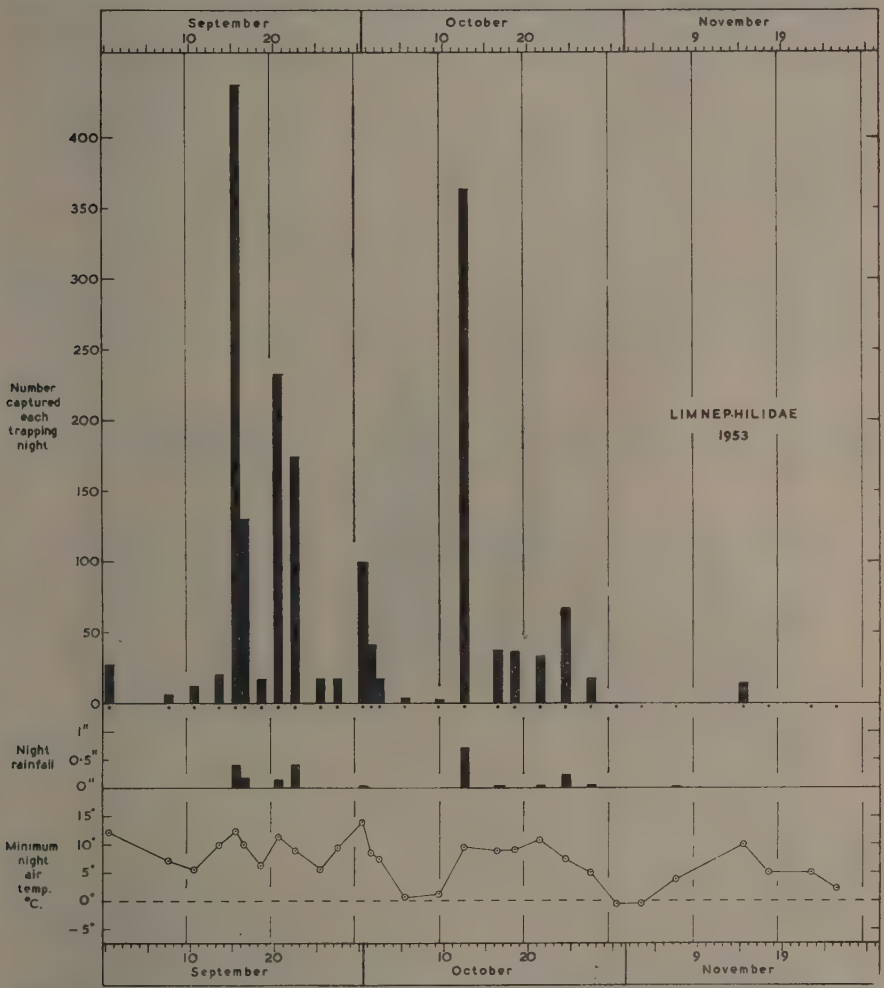

FIG. 7.—Captures of Limnephilidae in autumn 1953, with records of night rainfall at Grazeley and minimum night temperatures at Shinfield. The nights on which the trap was operated are indicated by dots below the abscissa.

these species overwinter as adults. On the other hand, caddis flies are present from April to November, and the number caught in the light trap is largely dependent on weather conditions. It has already been shown that *Agraylea multipunctata* was present in April and May, but was not trapped until the middle of June.

Caddis flies are capable of drinking water and nectar, but recorded observations of their feeding at flowers in the field are comparatively few and confined mainly to larger species, such as the limnephilids (Crichton, 1957). Döhler (1914) kept specimens of *Limnephilus flavicornis* alive for several weeks when he supplied them with

water, and for much longer with sugar solution. From the recapture of marked specimens I shall give evidence, to be published elsewhere, that limnephilids live for several weeks under natural conditions in the field. Having thus established that limnephilids are not short-lived, fluctuations in numbers captured on successive nights must be mainly due to variations in their activity and not to sudden emergences of short-lived species as would be the case with Ephemeroptera.

Williams (1940) has shown how the activity of insects is determined by weather conditions. As very large catches were made on comparatively few nights, they had

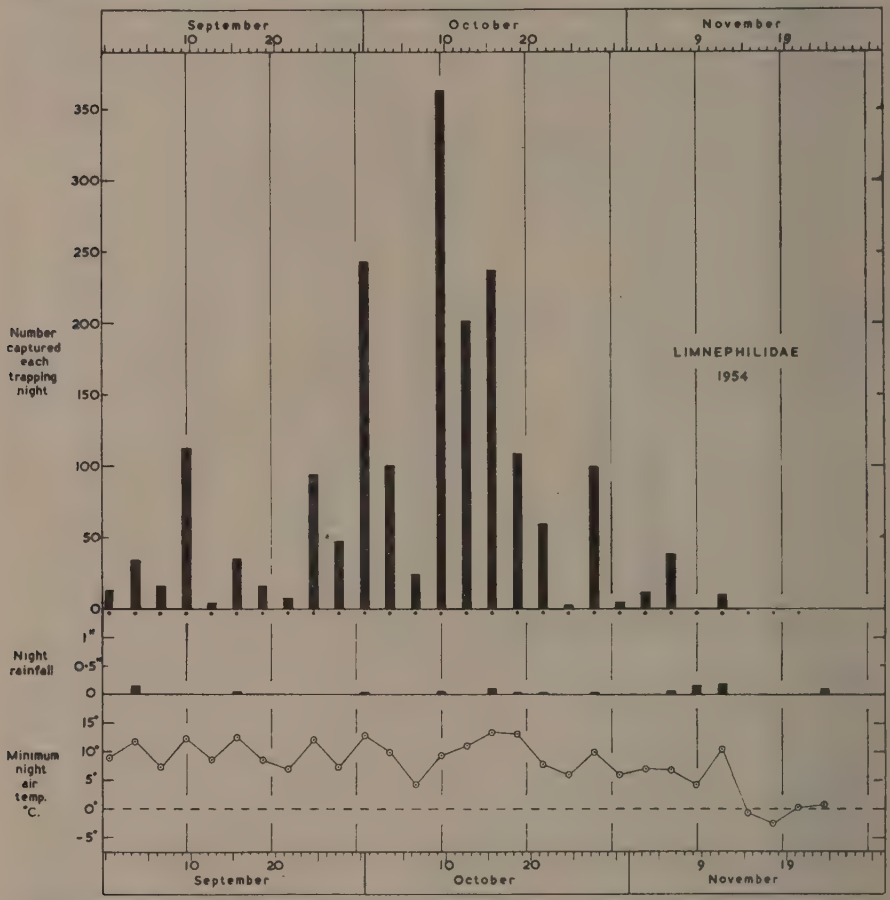

Fig. 8.—Captures of Limnephilidae in autumn 1954, with records of night rainfall at Grazeley and minimum night air temperatures at Millbarn Pond. The nights on which the trap was operated are indicated by dots below the abscissa.

a swamping effect on an arithmetic mean, so he expressed his catches as logarithms in order to obtain a geometric mean. This gave a more even distribution of nights on each side of the mean. Williams calculated that, on successive nights, an increase in the minimum temperature of 2·8° C. approximately doubled the catch. The nights of big catches at Rothamsted were those of higher temperature, little or no wind, and a high barometric pressure. As there was rain on about the same number of nights with large catches as with small ones, rainfall appeared to have no effect. Williams' work was concerned mainly with Diptera and Lepidoptera, which formed 97 per cent. of the total catch.

I shall consider here the numbers of Limnephilidae caught in September, October and November in relation to weather conditions. The total captures of all species of Limnephilidae for the years 1953, 1954, 1955 and 1957, together with records of night rainfall and minimum night air temperature, are presented in figures 7, 8, 9 and 10. Temperatures were not recorded at the site in 1953, and those shown in figure 7 are from Shinfield, 4 miles away and the same height above sea level. A comparison of minimum temperatures at Shinfield and Millbarn Pond in the autumns of 1954 and 1955 showed conditions to be closely comparable. During the autumn of 1957, a continuous record of night temperature and humidity was kept with a recording thermohygrograph. Over the 72 nights of trapping, the average temperature was 7·7° C. and the average minimum temperature was 6·1° C. The greatest difference during one night between average temperature and minimum temperature was 3·2° C. As the temperature changes during the night at this time of year are thus shown to be small, the minimum may be taken as a suitable measure of temperature. Figures 7, 8, 9 and 10 reveal that the large catches were made on the warmer nights. A further feature is that, with few exceptions, the largest catches were made on rainy nights. These catches are listed in Table VII which shows that on every night except one there was rain, often heavy and prolonged. *L. lunatus*, with 1,564 specimens, was the dominant species, being followed by *L. flavicornis*, *G. pellucidus* and *H. digitatus*.

TABLE VII.—*Large catches of Limnephilidae at the waterside site A in September and October* 1953, 1954, 1955, *and* 1957, *arranged in order of decreasing numbers*

Number of Limnephilidae	Date	Minimum night air temp. (°C.)	Rainfall in inches	Notes on weather during night
437	15/16.ix.53	12	0·40	Heavy rain all night.
363	12/13.x.53	9	0·69	Heavy rain after 21.00 hrs.
363	9/10.x.54	9	0·05	Light rain later in night.
243	30.ix/1.x.54	13	0·03	Light rain in night.
239	23/24.ix.57	12	0·83	Heavy rain all night.
237	15/16.x.54	13	0·10	Rain later in night.
232	20/21.ix.53	11	0·14	Heavy rain later in night.
201	12/13.x.54	11	.	No rain, mainly cloudy.
174	22/23.ix.53	9	0·40	Heavy rain later in night.
162	21/22.ix.55	15	0·04	Rain later in night.
130	16/17.ix.53	10	0·18	Rain later in night.

Although trapping was carried on for the same number of nights, the total catch of limnephilids in 1955 was noticeably smaller than in 1954. Thus, while in September, October and November 1954, the catch was 1,877, in 1955 it was only 484. In 1954, the average minimum temperature over these nights was 7·8° C., while in 1955 it was 5·8° C. The difference was most striking in October when the 1955 catches were very small and the average minimum temperature was only 3·2° C. against 9·4° C. in 1954. Also there were fewer wet nights in 1955. September and October were thus the months of greatest activity for these limnephilids. By November, they were dying off, and the lower night temperatures inhibited the activity of the survivors. The November catches have, therefore, been omitted from the analysis of variance which has been carried out on the logarithms of catches of limnephilids in September and October for the four years. The method of analysis was that of the weighted sums of squares (Snedecor, 1946). The catches were grouped into nights of rain or no rain, and into six minimum temperature groups of 3° and 4°, 5° and 6°, 7° and 8°, 9° and 10°, 11° and 12°, 13° and 14° C. The analysis is displayed in Table VIII.

TABLE VIII.—*Analysis of variance of the catches of Limnephilidae in September and October* 1953, 1954, 1955 *and* 1957 *in relation to temperature and rainfall*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Temperature .	5	8·74	1·75	7·14
Rainfall . .	1	3·60	3·60	14·70
Interaction .	5	1·30	0·26	1·06
Residual . .	93	22·78	0·25	.
Total .	104	47·55		

While interaction is not significant, both temperature and rainfall are significant at the 1 per cent. level. Thus, while there are larger catches on the warmer nights, only when there is rainfall on these nights are the very large catches made.

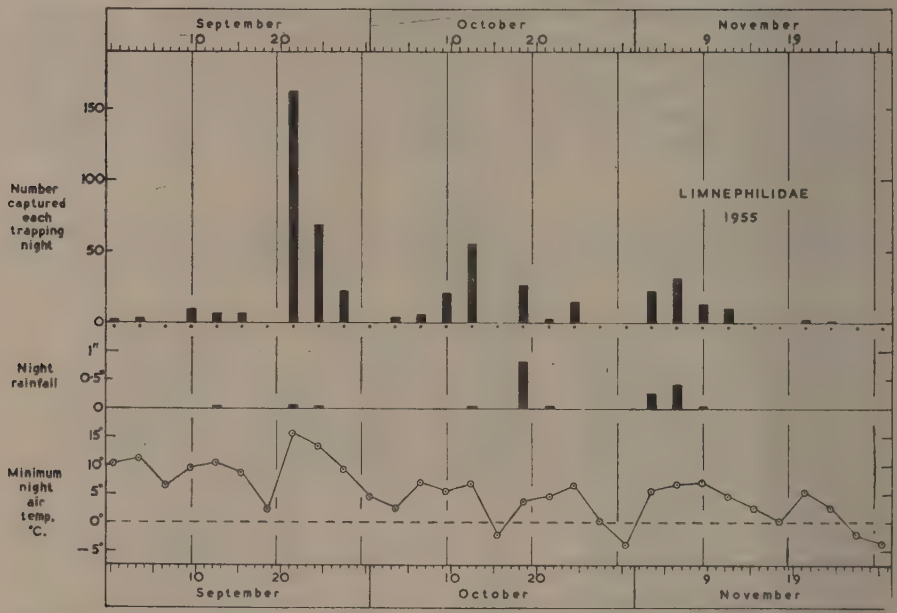

FIG. 9.—Captures of Limnephilidae in autumn 1955, with records of night rainfall at Grazeley and minimum night air temperatures at Millbarn Pond. The nights on which the trap was operated are indicated by dots below the abscissa.

On these autumn nights, the relative humidity is consistently very high. This was clearly shown in the hygrograph records for September and October 1957, when the average relative humidity never fell below 90 per cent., and for most of the nights, irrespective of rainfall, the instrument recorded saturation. Relative humidity cannot be regarded as an important factor in relation to the numbers of limnephilids caught.

During the autumn of 1957, a second light trap was operated at site B about 70 yards away from site A, and shielded from it by a screen of trees. Although hidden from the water, the field trap caught almost as many limnephilids as the waterside trap. For both traps the largest catches were on the same wet nights of 23rd/24th September and 10th/11th October.

The larger limnephilids are often recorded in light traps some distance from water. The note by de Worms (1953) is of particular interest here. Although his trap at Woking, Surrey, was about a mile from water, on the night of 24th September 1952

he caught about 200 caddis flies. In a sample from this catch the following species, all limnephilids, were identified: *Limnephilus flavicornis*, *L. marmoratus*, *L. sparsus*, *L. auricula*, *Grammotaulius atomarius* and *Stenophylax permistus*. The night was warm and windy, with a certain amount of rain. Another collector, 10 miles away at Weybridge, had a similarly large catch of caddis flies on the same night. De Worms informed me (*in litt.* 21.x.56) that, although he had run his light trap regularly since then, this was the only occasion on which he had collected such a large number of caddis flies.

A further example of a large catch of limnephilids on a wet night is provided by trapping which I carried out, close to the water, at Flatford Mill, Suffolk on six successive nights from 10th September, 1958.

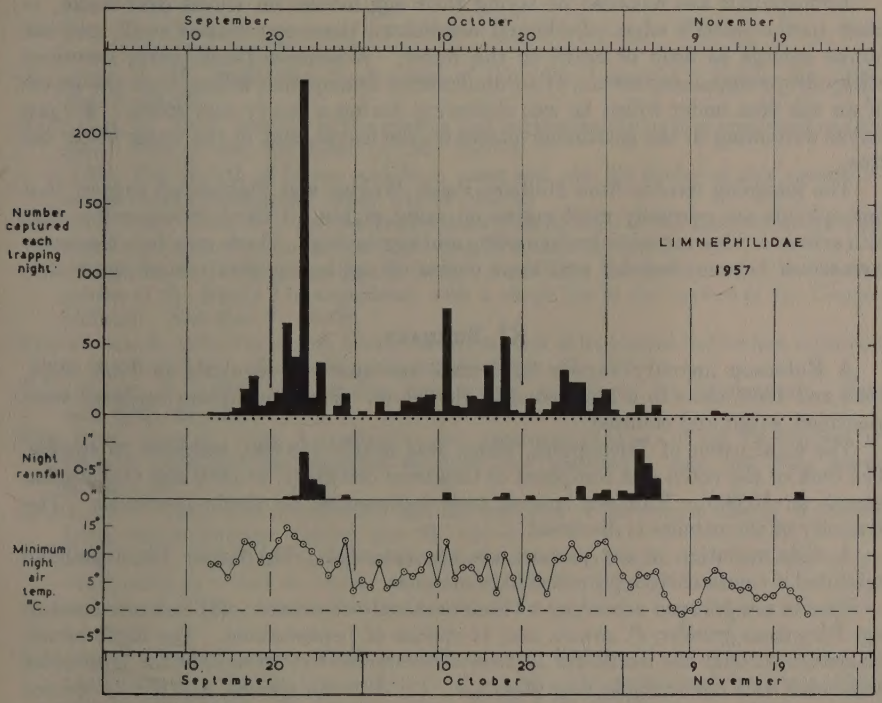

FIG. 10.—Captures of Limnephilidae in autumn 1957, with records of night rainfall and minimum night air temperatures at Millbarn Pond. The nights on which the trap was operated are indicated by dots below the abscissa.

TABLE IX.—*Catches of Trichoptera and other orders of insects at Flatford Mill, Suffolk, 10th–16th September* 1958

	10/11.ix	11/12.ix	12/13.ix	13/14.ix	14/15.ix	15/16.ix
Trichoptera—limnephilids .	26	11	17	6	562	40
,, other families	27	12	12	20	85	44
Other orders . . .	832	1,324	975	669	1,855	1,605
Night rainfall (in.) . . .	.	.	.	.	0·16	.
Minimum night air temperature (°C.)	9·8	10·0	10·7	9·8	12·5	10·5

From Table IX it can be seen that on the night of 14th/15th September an exceptionally large catch of Limnephilidae was made, but the numbers of other

Trichoptera and of insects of other orders were not much greater than on the other nights. The dominant limnephilid was *Limnephilus affinis*, while other species present were *L. flavicornis*, *L. marmoratus*, *L. lunatus*, *L. auricula* and *Stenophylax permistus*. The minimum temperature was only a little higher than on the other nights, but this was the only night on which rain fell (0·16 inch in a brief thunderstorm). A comparable large catch of limnephilids was made in a second trap which was run concurrently each night in a field about 100 yards away, screened from the river by a belt of trees.

Marshall (1939) collected only a few limnephilids when trapping at Lake Erie in 1938. This may perhaps be explained by the fact that she did not use the light on rainy nights.

Limnephilids are recorded as laying their egg masses on leaves over water, or close to the water's edge. In humid conditions, these egg masses swell, and the larvae emerge to drop or crawl to the water. Wesenberg-Lund (1913) described sticky drops containing larvae, of an unidentified limnephilid, falling from the leaves of an ash tree under which he was sheltering during a heavy rain storm. He saw larvae swimming in the gelatinous masses on the leaves, and in the water below the tree.

The foregoing records from Millbarn Pond, Woking and Flatford all suggest that limnephilids are normally most active on rainy nights. I think it is possible that rain acts as a releasing stimulus to mating and egg-laying. There may be a necessary connection between rainfall and their choice of egg-laying sites out of the water.

XI. Summary

A Robinson mercury vapour light trap was operated regularly in 1953, 1954, 1955 and 1957, close to a large pond in Berkshire. The Trichoptera captured were identified, sexed and counted.

The total catch of Trichoptera, which was nearly 115,000, included 70 species. The bulk of the catch was composed of *Oxyethira costalis* (*c.* 81,000) and *Orthotrichia tetensii* (*c.* 13,000). Thirteen species were represented by single specimens. The diversity of the catches is discussed.

A wide variation in sex proportions was recorded. The family Limnephilidae exhibited a consistently high percentage of males.

Species are grouped according to their seasonal occurrence : (1) Summer species, e.g. *Phryganea grandis*, *P. striata*, and 14 species of Leptoceridae. The flight period ranged from about one month for *Leptocerus tineiformis* to four months for *Mystacides longicornis* and *Hydropsyche angustipennis*. (2) Autumn species, e.g. the 24 species of Limnephilidae. (3) Double-brooded species, e.g. *Oxyethira costalis*, and possibly *Agraylea multipunctata* and *Tinodes waeneri*.

The autumn catches of Limnephilidae are related to weather conditions. There was rainfall on every night except one of the eleven on which the largest catches were made. From an analysis of variance, both temperature and rainfall are shown to affect the numbers caught significantly at the 1 per cent. level. It is suggested that these limnephilids are most active on rainy nights.

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